西藏地衣物种多样性的海拔梯度分析*

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摘要:根据西藏地衣分类和区系的文献资料,对西藏地衣物种多样性的海拔梯度进行了分析。267 个分类群按照生长型或者基物被分为六组。每一组地衣的物种丰度随海拔增加呈现单峰曲线形式的变化。多数组物种丰度的峰值出现在海拔3400~3900 m之间,对应于山地寒温带针叶林带的上半部分,比尼泊尔对应类群出现极值的海拔要高。此植物带谱内复杂的生态系统可能是物种多样性高的主要原因。壳状地衣物种丰度的峰值出现在5100~5400 m区间则可能是因为该区内高大的树木的消失以及具有充裕的阳光。西藏的地衣物种多样性远低于尼泊尔,两地共有的物种数量很少。对西藏地衣物种多样性的调查不充分应当是其主要原因,因此今后中国地衣学工作者应当加强西藏地衣多样性的研究。

关键词: 物种丰度; 海拔; 西藏; 单峰模型

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Altitudinal Gradients of Lichen Species Richness in Tibet, China

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Abstract: Altitudinal gradients of lichen species richness in Tibet, China were investigated based on taxonomic and floral literatures. Two hundred and sixty-seven lichen taxa were classified into six groups based on their growth-forms or substrates. The species richness of all groups varied according to altitudinal gradient in a unimodal way. The maximum species richness of most lichen groups were detected between 3 400–3 900 m, corresponding to the upper part of montane boreal coniferous forest, and the extreme height of the occurrence of theses lichen groups in Tibet is higher than that in Nepal. This was probably due to the complex ecosystems in this vegetation zone. The species richness of crustose lichens reached its peak at 5 100–5 400 m, which may be attributed to the disappearance of trees and ample sunlight. However, comparisons showed that the species diversity in Tibet was much lower than that in Nepal. This suggests poor understandings of lichen diversity in the area, and further investigations are need.

Key words: Species richness; Altitudinal; Tibet; Unimodal

Altitudinal patterns of species diversity are of particular importance in theoretical and applied ecology as well as in conservation biology (Sergio and Pedrini, 2007; Pryke and Samways, 2010). The

relationships of species richness and elevation were investigated by various authors in various areas yet different patterns were found (Rohde, 1992; Grytnes *et al.*, 2006). Some researchers reported that

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species richness decrease with increasing altitude (MacArthur, 1972; Rohde, 1992), while others argued that species richness increase with increasing altitude until they reach their maximum at the middle elevation and then they decrease with increasing altitude (Grytnes et al., 2006; Pinokiyo et al., 2008). Tibet is the highest area in China, vegetation zonations are obvious and distinctive there, and this study aimed to determine the altitudinal patterns of lichen there.

Prof. Wei Jiang-Chun took part in the scientific expedition in Tibet, China, organized by Chinese Academy of Sciences about four decades ago. He and other scientists collected a great deal of lichen specimens during the expeditions, and the reports on taxonomy and flora based on these specimens were published subsequently. These publications are cited here as data source of vertical range of species.

1 Investigation areas and the vegetation zonations

The study areas are exactly the same as in Wei and Jiang (1986; Fig. 1 therein), covering from the Qamdo, Zogang regions and Zayu in the East and Gyirong in Shigatse regions in the West, to the Cona, Yadong and Nyalam regions in the South and the Lhasa, Nagqu and Baen regions in the North, corresponding to E85°18.43′-97°50.20′, N27°28.44′-31°55.29′. The altitude of this area is between 1 680 m a. s. l. and 6 100 m a. s. l. Seven vegetation zones were recognized in this area as following, and compositions and structures of higher plants and lichen populations vary in different zones accordingly (Wei and Chen, 1974; Zheng and Chen, 1981; Wei and Jiang, 1986).

Subtropical evergreen broad-leaved forest is elevated from 1 600 m to 2 500 m. In this zonation, Castanopsis hystrix and Cyclobalanopsis kiukiangensis are the constructive and dominant higher plants, while Parmotrema tinctorum, Parmelina wallichiana, Cetrelia pseudolivetorum and Usnea arborea are the common lichen species there.

Montane temperate mixed forest ranges from 2 500 m to 3 100 m, and *Tsuga dumosa* is the dominant species there. The most abundant lichen species in this zone are *Parmelina irrugans*, *Parmelina aurulenta*, *Cetraria pallescens*, *Ramalina sinensis*, *Cladonia aggregate*, etc.

Abies delavayi and Ab. delavayi var. motuoensis dominate at montane boreal coniferous forest (3 100 –3 900 m), and Rhododendron basilicum, Rh. wardii and Acanthopanax evodiaefolia occupy the understory. Thus, the community structure is rather complicated. At this range, the lichen species diversity is most abundant. Alectoria acanthodes, Bryoria smithii, Usnea longissima, U. thomsonii, Punctelia borreri, Parmotrema arnoldii, Parmelia grayana, Menegazzia terebrata, Cladonia gracilis, Peltigera scabrosa, Umbilicaria indica, etc. are the main species here.

Flowering plants, such as *Rh. campylogynum*, *Salix oreophila*, *Cassiope wardii*, etc. are the main components of subalpine boreal shrubs and meadows (3 900–5 000 m), while *Juncus bracteatus*, *Polygonum viviparum*, etc. are components of alpine meadow belt (5 000–5 600 m), no tall trees appear here and beyond. The common lichen species at these two zonations are *Evernia mesomorpha*, *Parmelia saxatilis*, *Thamnolia vermicularis*, etc.

The alpine lichen belt (5 400–6 100 m) is between alpine meadow belt and alpine nival belt (above 6 100 m). At this zonation, mean annual temperature is between –4 °C and –8 °C, and soil is poorly developed, higher plants are seldom seen. Thus lichens especially the crustose ones dominate at this zone. Lecidea auriculata, Rhizocarpon superficiale, Lecanora polytropa, Th. vermicularis, etc. are the most dominant species at this belt.

2 Data and methods

The elevation data adopted in this study were obtained from the literatures exclusively (Wei and Chen, 1974; Wei and Jiang, 1980, 1982, 1986). Lichen nomenclature followed Wei (1991). We grouped

these data according to growth forms and substrates. Crustose, foliose and fruticose lichens were considered to be their own natural groups according to growth forms, and corticolous, saxicolous and terricolous lichens were grouped according to their substrates. As an intermediate growth form, the squamulose lichens were grouped into crustose lichens. Lichens growing on twigs, stumps, trunks and barks were recognized as members of corticolous group, while those growing on soil, grasses and mosses were grouped into terricolous group.

Two principles were introduced to deal with these data. Firstly, the lowest elevation for each taxon was lowered by 10% from the original data in literatures, while the highest elevation was heightened by 10%. After all, data from literatures were not as accurate as from sample investigations. The collectors may not be biased and collected whatever they met in collection activities, but it was very impossible for them to collect the specimen of every taxon at its lowest or highest limits of distribution. In addition, many taxa reported in the literatures were cited only one or two specimens for each. This situation made us very difficult to determine their lowest and highest elevation, and thus, such adjustment was necessary. Secondly, we assumed that, each taxon was distributed consecutively between its two extreme elevations. That was, if we found a species at 1 000 m and 2 000 m, then we regarded that it also occurred at every 100 m band in this altitudinal range. The necessary of this assumption, we called "continuity assumption", was self-evident, because there were many taxa reported in literatures, which were cited only two or three specimens for each in a large altitudinal range, and it was unlikely that such taxa were distributed at their two extreme elevations only.

Despite the obvious necessity of these two principles, we carried out partial correlation tests controlling for the effect of elevation between two data sets for each group to evaluate whether these two principles were reasonable; one set was the number

of taxa in each 100 m belt derived according to these two principles (referred as derived data hereafter), the other was the number of taxa in each 100 m belt that exactly recorded in literatures (referred as original data hereafter).

According to these two principles, we divided the whole altitudinal range of the investigated areas into 53 consecutive zones, with each zone covering 100 meters. To be convenient, all species, subspecies, varieties, and forms were treated as different species, and species richness were estimated by counting the total number of all taxa occurring in each 100 m band. Thus gamma diversity *sensu* Whittaker (1972) were dealt in this study. These treatments were processed in Microsoft Office Excel 2003. The obtained data then were transferred to SPSS 16.0 for Windows (SPSS Incorporated, Chicago, Illinois) for further analyses, which included plotting and correlation analyses.

Lichens in Nepal (Baniya et al., 2010) were also integrated into this study in order to make a comparison between the altitudinal patterns of lichens from these two areas.

3 Results and discussion

Totally we collected data for 267 lichen taxa (actual number of species was 228) represented 58 genera from Tibet, China, distributed between 1 680 m a. s. l. and 6 100 m a. s. l. The number of taxa and altitudinal range of each group can be seen in Table 1. Crustose lichens had the least abundant species and they also occupied the highest altitudinal ranges, while foliose lichens had the most abundant species and saxicolous lichens were distributed throughout the investigated altitudinal ranges.

Results of partial correlation tests for the original data and derived data can be seen in Table 2. Except for the crustose group, the data in other groups were strongly correlated, which also can be referred from the similarities between the topography of their histograms of original data and scatter plots of derived data (Figs. 1, 2). The low correlation

occurring in crustose lichens probably is because too few species were adopted in analysis. In any case, our two principles got a solid support from statistics and were applicable in following analyses.

Table 1 Number of taxa and altitudinal range in each group of lichens in Tibet, China

Groups	No. of taxa	Al.: 1: 1 a /	Altitudinal range of the peaks of	Altitudinal range of the	
		Altitudinal range ^a /m	species richness in ${\sf Tibet}^b/{\sf m}$	peaks in Nepal ^c /m	
Crustose	22	2 850-6 100	5 100-5 600	4 100-4 200	
Foliose	155	1 680-5 667	3 400-3 800	2 400-2 500	
Fruticose	89	1 800-5 800	3 400-3 900	3 200	
Corticolous	118	1 680-5 800	3 400-3 800	2 500-2 700	
Saxicolous	76	1 680-6 100	3 400-3 700	3 900-4 200	
Terricolous	90	2 050-5 700	3 500-3 900	3 900-4 200	
Total^d	267	1 680-6 100	3 500-3 900	3 100-3 400	

Note: ^aOriginal data; ^baccording to derived data; ^cdata from Baniya *et al.* (2010); ^dthe sum of number of species of growth-form-based groups is little larger than the number of total species for some species have more than one growth forms; it is also true for the groups based on substrate

Table 2 Partial correlation tests for original and derived data of each group *

Group	Fruticose	Foliose	Crustose	Terricolous	Saxicolous	Corticolous
Coefficient	0.736	0.760	0.235	0.748	0.694	0.788
2-tailed sig.	< 0.01	< 0.01	0.181	< 0.01	< 0.01	< 0.01

Note: * Controlling for the effect of altitude

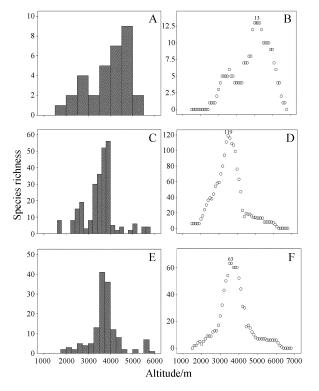


Fig. 1 Histograms and scattered plots of species richness of crustose, foliose and fruticose lichens along altitude.
Left: histograms of original data; right: scatter plots of derived data. A-B: crustose lichens; C-D: foliose lichens; E-F: fruticose lichens

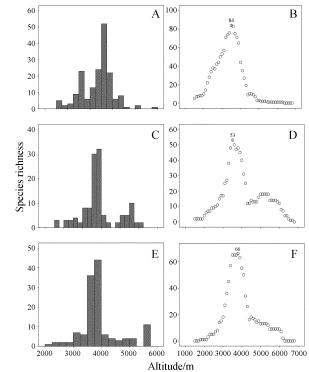


Fig. 2 Histograms and scattered plots of species richness of corticolous, saxicolous and terricolous lichens along altitude.
Left: histograms of original data; right: scatter plots of derived data. A-B: corticolous lichen; C-D: saxicolous lichens; E-F: terricolous lichens

Baniya et al. (2010) cited 524 lichen taxa to investigate the altitudinal gradient of lichen species richness in Nepal from literatures. These lichens were distributed between 200-7 400 m, occupying a much larger altitudinal range than that in this study. Among these taxa, eighty were common in Tibet and Nepal, the similarity coefficient was rather small (0. 10 sensu, Sorensen, 1948). Among them, 43 were distributed in the similar altitudinal ranges or partly overlapped at least. There were 11 taxa distributed at higher elevations in Nepal than in Tibet, while 26 other taxa were lower. For the lichens species in Nepal, 487 were distributed between 1 680 m and 6 100 m, an altitudinal range corresponding to that in this study. There were 63 species shared by Tibet and Nepal at this range, which made the similarity coefficient further lower (0.08). This low similarity may be partly attributed to different composition of lichen flora due for complete difference of ecological environments in these two areas. But the underestimated species diversity for these two areas, especially for Tibet, is also an important reason. Though R. P. David had a field trip to Tibet as early as the year of 1869, and Zahlbruckner and other lichenologists reported some species from Tibet, it was until 1980s that Prof. Wei made systematic investigations on the flora (Wei, 1991 and citations therein). Later, few taxonomic and floral studies were made concerning this area, and the resulted underestimation of species diversity was not surprising.

The total species richness showed a unimodal pattern according to altitudinal gradients, with its peak at 3500-3900 m, whereas the observed maximum richness (187 taxa) was at about 3 600 m (Fig. 3, Table 1). The maximum species richness of crustose lichens was at 5 100-5 600 m, that of foliose lichens was at 3 400-3 800 m, while that of fruticose lichens was at 3 400-3 900 m (Fig. 1, Table 1). The maximum species richness of terricolous lichens was at 3500-3900 m, that of corticolous lichens was at 3 400-3 700 m, while that of saxicolous lichens was at 3 400-3 800 m (Fig. 2, Table 1). It was obvious that, except for the crustose group which reached its peak of species richness at much higher elevations, the altitudinal patterns of species richness of the other five groups were highly accordance with the total species richness which was supported by correlation tests (Table 3). The topography of their scattered plots along the altitude also resembled to each other (Fig. 3).

The peak of species richness of each group fell into different altitudinal ranges in Tibet and Nepal (Table 1). Both in Tibet and Nepal, the maximum species richness of crustose lichens was at the highest elevations among these six groups. But it was somewhat surprising that, except for terricolous and

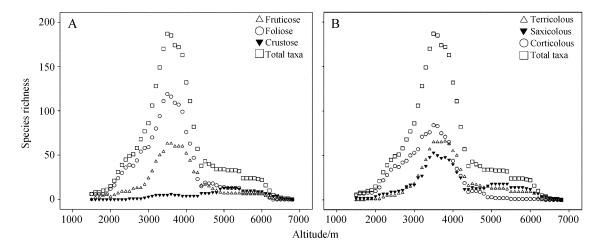


Fig. 3 Scattered plots of total species richness along altitude. Scattered plots of the 6 groups are also reproduced here to make convenient comparisons

Table 3 Correlation tests for the altitudinal distributions of total species and six groups

Group	Terricolous	Saxicolous	Corticolous	Fruticose	Foliose	Crustose
Tatal taxa	0.973	0.972	0.953	0.983	0.988	0.016
2-tailed sig.	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.908

saxicolous groups, the species richness reached their peaks at lower elevation in Nepal than in Tibet. Maybe it can be explained by the more complicated micro-ecological conditions in Tibet. What it may be, this results was accordance with the low similarity of lichen diversity between this two areas.

The peaks of species richness of the groups, except for crustose group, fell into the upper part of the mountain boreal coniferous forest (3 400-3 900 m). This result coincided with the geographical element analyses by Wei and Jiang (1986). This was because the factors of latitudinal zonality have been weakened here due to the continuously elevation of Tibet Plateau, and the distributions of organisms were strongly effected in turn. The fruticose and terricolous lichens had obvious plateaus at this belt (Fig. 3). Below this belt, the total species richness increased rapidly with the increasing elevation. This may be mainly attributed to the increase of species richness of foliose lichens or corticolous lichens (Fig. 3). Species richness of other groups increased relatively slowly. The species richness of crustose lichens remained in a low plateau until the elevation reaches 3 000 m and thus made less contribution to the increase of total species richness. Above the mountain boreal coniferous forest, the total species richness decreased steeply with increasing elevation until the elevation reached ca. 4800 m where it arrived a plateau (Fig. 3). This phenomenon was induced by the dramatic decrease of the species richness of all groups except the crustose one. The species richness of crustose lichens, on the contrary, slightly increased from 3 800 m to 5 400 m and arrived its maximum there and then decreased slowly with increasing altitude. The species richness of saxicolous lichens also increased slightly at 4 300-5 400 m and formed a secondary peak there, but this

didn't influenced the drastic decline of total species richness. This increase of species richness of saxicolous lichen in this altitudinal range may be due to the disappearance of trees and the exposure of rocks to sunlight.

As a whole, the species richness of all groups had a unimodal altitudinal pattern. This pattern has been reported by many other authors in different organisms (Bruun *et al.*, 2006; Grytnes *et al.*, 2006; Pinokiyo *et al.*, 2008; Huang, 2010). It is characterized by a peak of species richness at intermediate altitudes. However, a slightly bimodal peak was detected for saxicolous lichens (Fig. 2: D) between 4 800 – 5 600 m, the transition from alpine meadow to lichen belt. Baniya *et al.* (2010) also detected bimodal peaks for saxicolous and terricolous lichens in Nepal. These secondary peaks are probably induced by complex ecological environments in a local scale, and it doesn't influence the topography in a whole.

4 Conclusions

Altitude is believed a key factor to determine the patterns of biodiversity (McCune et al., 1998; Sergio and Pedrini, 2007). Lichens are important indicators of air quality and forest health (McCune, 2000; Jovan and McCune, 2006) and their altitudinal patterns have been received some attentions recently. Based on Prof. Wei's significant works on lichen taxonomy and flora of Tibet, our analyses suggested the lichen species richness were peaked in the mountain boreal coniferous forest.

However, much less taxa were reported from Tibet than from Nepal, and there were only a few taxa common in these two areas. This phenomenon may be explained by the different ecological conditions partly, but it is also necessary to point out that the flora of Tibet is seriously underestimated and thus deserves intensive investigations in future.

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